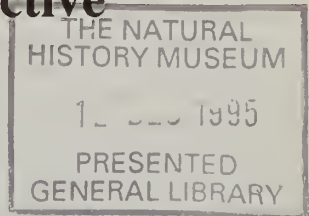


# Preliminary studies on a mandibulohyoid 'ligament' and other intrabuccal connective tissue linkages in cirrhitid, latrid and cheilodactylid fishes (Perciformes : Cirrhitidae)



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**SYNOPSIS.** In certain taxa of at least three groups of percomorph fishes belonging to the cirrhitoid families Cirrhitidae and Latridae, there is a connective tissue linkage between the mandible and the hyoid arch, suggestive of the mandibulohyoid ligament described in certain sub-percomorph groups. This ligament is generally thought to be a feature of lower teleost fishes, although a mandibulohyoid connection has also been identified in a few more derived taxa. The mandibulohyoid connection in the Cirrhitidae examined would appear to originate from the tendinous aponeurosis associated with the Aw division of the adductor mandibulac muscles, but its derivation in the latrid species *Acantholatris monodactylus* remains undetermined. The Aw aponeurosis in *A. monodactylus*, as well as in the latrid *Mendosoma*, and in two genera of Cheilodactylidae (*viz. Chirodactylus* and *Cheilodactylus*) ramifies extensively over the palatoquadrate arch and part of the opercular series. This system, together with various intrabuccal ligaments is described from representatives of the three cirrhitoid families studied.

It is concluded that, contrary to several earlier ideas, a mandibulohyoid linkage is of taxonomically and phylogenetically widespread occurrence in teleosts but that it might be derived from different connective tissue sources. The value of this connective tissue complex in phylogenetic studies has yet to be established, but it appears to be of use in at least establishing intragroup relationships within the Cirrhitoidci.

## INTRODUCTION

A recent anatomical study of certain cirrhitoid fishes (*sensu* Greenwood, 1995) has revealed a number of markedly different ligament and tendon systems which separately or conjointly link the mandible with the hyoid arch, the palatoquadrate arch and the opercular series. Some of these connections have a degree of complexity not previously recorded among teleost fishes.

Of particular functional interest are the two types of direct

and ligament-like connections between the ceratohyal and mandible in some cirrhitid species, and a third type found in one of the latrid species examined (family placement after Greenwood, 1995). These linkages invite comparison with the so-called mandibulohyoid ligament generally thought to be commoner in lower teleosts than in perciform taxa, or even restricted to the former groups (see Verraes, 1977; Lauder & Liem, 1980; Lauder, 1982; but see also Osse, 1969; Springer *et al.*, 1977, and Aerts *et al.*, 1987 for certain perciforms, and Anker, 1974, for gasterosteiforms). A mandibulohyoid ligament also occurs in the semionotiform lepisosteids *Lepisosteus* and *Atractosteus* (Wiley, 1976).

<sup>†</sup> Dr Greenwood died 3 March 1995.

The nature of the hyoid-mandibular connection in the cirrhitoids, a derived percomorph group (Greenwood, 1995), and that described in other teleosts and in the Lepisosteidae, raises doubts about the strict homology of the connection in these various taxa.

Functionally, it would seem that a mandibulohyoid connection is of importance both in adults (see Aerts *et al.*, 1987) and in early larval stages (Verraes, 1977); its phylogenetic history in this context is discussed at length by Lauder (1982).

Regrettably, the feeding studies on cirrhitoids, from which this anatomical study arose, are not sufficiently advanced or refined to allow informed speculation on any correlation between the morphology and the feeding habits of these fishes. Furthermore, many other cirrhitoid taxa remain to be studied before it will be possible to evaluate what significance the different types of intragroup mandibulohyoid and other linkages (or absence thereof) may have in unravelling the taxonomy and phyletic relationships of the group. Nevertheless, there are indications from this study, and from information in the literature on various forms of mandibulohyoid connections, that further investigations may yield insight into the biomechanics of feeding and into historical relationships.

## MATERIALS AND METHODS

### Material

Clupeidae:	<i>Etrumeus terres</i> . RUSI 34140 (1 specimen)
Salmonidae:	<i>Oncorhynchus mykiss</i> RUSI 36417 (3 specimens)
Characidae:	<i>Hydrocynus vittatus</i> RUSI 19355 (1 specimen)
Cirrhitidae:	<i>Amblycirrhitus bimacula</i> RUSI 77-20 (3 specimens)
	<i>Cirrhitichthys oxycephalus</i> RUSI 40526 (3 specimens)
	<i>Cirrhitops fasciatus</i> RUSI 2375 (1 specimen; ex Hawaii)
	<i>Cyprinocirrhites polyactis</i> RUSI 12339 (3 specimens)
	<i>Paracirrhites arcatus</i> RUSI 30975 (2 specimens)
	<i>Paracirrhites forsteri</i> RUSI 39419 (3 specimens)
Latridae:	<i>Acantholatris monodactylus</i> RUSI 33485 (2 specimens)
	<i>Mendosoma lineatum</i>
	RUSI 33613 (1 specimen)
	RUSI 33626 (1 specimen)
	RUSI 26176 (1 specimen)
Cheilodactylidae:	<i>Cheilodactylus fasciatus</i> DIFS unreg. (2 specimens)
	<i>Cheilodactylus pixi</i> DIFS unreg. (3 specimens)
	<i>Chirodactylus brachydactylus</i> DIFS unreg. (3 specimens)

DIFS: Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown. RUSI: J.L.B. Smith Institute of Ichthyology, Grahamstown.

### Method

The entire opercular series, palatopterygoid arch and hyoid arch of one side, together with the mandible, premaxilla and maxilla of that side, were dissected away from the head. Muscles, tendons and ligaments were examined on the dissected side, and checked on the contralateral aspect which was left *in situ*.

All specimens had been fixed in formalin and preserved in either ethyl or propyl alcohol.

In the absence of ontogenetical information on the development of ligamentous and tendinous systems in these fishes, ligaments and tendons in the various taxa are presumed to be homologous if their places of origin and insertion are similar.

## ABBREVIATIONS FOR FIGURES

Abbreviations for tendons and ligaments are given separately with each figure.

### Muscles:

Add. mand.

I u & m: Adductor mandibulae A<sub>1</sub> upper and main divisions respectively

Aw: Aw division of adductor mandibulae muscle

Awt: Tendinous aponeurosis of adductor mandibulae Aw

Geh: Geniohyoideus

Im: Intermandibularis

St: Sternohyoideus

### Skeletal elements:

Ang: Anguloarticular

Bb: 1st basibranchial

Ch: Ceratohyal

Dt: Dentary

Ect: Ectopterygoid

Ent: Entopterygoid

Epi: Epihyal

F: Raised facet for articulation with epihyal

Ga: Gill arch

Hyom: Hyomandibula

Hyp: Hypohyals

Ihyl: Interhyal

Iop: Interoperculum

Max: Maxilla

Mt: Metapterygoid

Pal: Palatine

Pop: Preoperculum

Q: Quadrate

R: Retroarticular

Sy: Symplectic

V: Vomer



## LIGAMENTOUS AND OTHER CONNECTIVE TISSUE LINKAGES BETWEEN THE MANDIBLE, THE PALATOQUADRATE, THE HYOID ARCH, AND THE OPERULAR SERIES IN THREE CIRRHITOID FAMILIES

### The family Cirrhitidae

On the basis of their mandibulohyoid connections, two distinct groups can be recognised within the cirrhitid species examined. A third group, represented by *Amblycirrhitus bimacula* (Jenkins), has no macroscopically detectable mandibulohyoid linkage (see below).

Group I species (*viz.* *Cyprinocirrhites polyactis* [Bleeker], *Cirrhichthys oxycephalus* [Bleeker] and *Cirrhitops fasciatus* [Bennett]) have a stout, ligament-like connection between the ceratohyal of each side and the coronoid process of the corresponding dentary ramus (Fig. 1A). Group II species (*viz.* *Paracirrhites arcatus* [Cuvier] and *P. forsteri* [Schneider]) also have a ligament-like band of tissue stemming from the lateral aspect of each ceratohyal, but here it links each hyoid arch with, predominantly, the corresponding quadrate, on which it inserts immediately above that bone's process for articulation with the anguloarticular. Part of this tissue, however, is apparently continuous with the tendinous insertion of the Aw division of the adductor mandibulae muscle, (Fig. 1C). There is no macroscopically obvious and clearly defined connective tissue linkage between the mandible and hyoid arch in *Amblycirrhitus bimacula* (hereafter referred to as Group III).

In all three groups the adductor mandibulae Aw division originates on the quadrate through a posterior extension of the muscle's tendinous central aponeurosis, and thus is of the basic perciform type as defined by Gosline (1986). The extension is well-demarcated and moderately deep, and lies across the quadrate-anguloarticular joint. *Amblycirrhitus bimacula* (the single Group III species examined) is exceptional in this respect because the tendon lies very slightly above the jaw articulation. Members of all three groups have the fascia covering the Aw muscle extending posteriorly onto the lower half of the quadrate, part of the preoperculum, and the upper margin of the interoperculum as well.

Within the three species of Group I there are differences in the association between the mandibulohyoid connection and the tendon of the adductor mandibulae  $A_1$  muscle inserting on the maxilla. *Cyprinocirrhites polyactis* is unique in having what appears to be a short branch of the mandibulohyoid connection arising near the latter's attachment to the coronoid process of the dentary and then joining the maxillary tendon of the adductor mandibulae  $A_1$  muscle (Fig. 1A). In *Cirrhichthys oxycephalus* and *Cirrhitops fasciatus*, the maxillary tendon partially fuses with the mandibulohyoid connection at the point where the two cross over each other (the latter lying medial to the maxillary tendon). From the point of fusion a short section (interpreted as a continuation of the maxillary tendon) runs into the tendinous central aponeurosis of the adductor mandibulae Aw muscle (Fig. 1B).

There are also intergroup differences in other ligamentous and tendinous linkages (Fig. 1). Species of Groups I and III have a small upper, anterior division of the adductor mandibulae muscle  $A_1$  inserting onto the maxilla only *via* the ligamentum primordium. Group II species, in contrast, have

that division of the muscle inserting on the maxilla through both the *ligamentum primordium* and the maxillary ligament of adductor mandibulae  $A_1$  muscle. In all three groups the major (*ie* lower) division of the muscle is attached to the *ligamentum primordium* and the maxillary ligament, the latter inserting on the ventral aspect of the maxilla, and the former on the bone's dorsolateral aspect.

Other intergroup differences involve the epihyal-interopercular and the interhyal-interopercular ligaments (For comparison of these and other ligaments with the situation in other cirrhitoid families, see pp. 94 and pp. 97–98 and Figs 2–4). Group II species have the latter ligament partly associated with the epihyal as well as the interhyal, as does the single Group III species dissected; in Group I taxa, however, the ligament is confined to the interhyal. The epihyal-interopercular ligament shows more marked intergroup differences, especially when species of Group I are compared with those of the other two groups, a difference possibly associated with the manner in which the epihyal contacts the interoperculum. In Group II taxa, the lateral face of the epihyal head articulates with a well-defined, prominently raised and posteriorly directed facet situated a little below the dorsal margin of the interoperculum and slightly behind the bone's midpoint. The epihyal-interopercular ligament in these fishes is short and stout, originates on the lateral face of the epihyal near its dorsal tip, and runs forward at approximately 45° to the sagittal plane. It inserts on the upper and anterior faces of the prominence supporting the facet on the interoperculum against which the epihyal articulates. A similar epihyal-interopercular ligament occurs in the single Group III species examined, *viz.* *Amblycirrhitus bimacula*. However, in this species, unlike those of Group II, the interopercular facet is located on a relatively lower base.

The epihyal-interopercular ligament is most distinctive in Group II. In species of this group (unlike the other groups) the epihyal articulates directly with the medial face of the interoperculum and not with a facet carried on a distinct and elevated base (albeit only slightly so in the single Group III species examined). The ligament itself is a prominent feature originating (as in other groups) on the dorsal tip of the epihyal's lateral face, from which it runs anteriorly onto the dorsal margin of the interoperculum at a point near the bone's anterior tip, where it is narrowly separated from the attachment point of the mandibulo-interopercular ligament (*cf.* *Acantholatris monodactylus* Fig. 3 & p. 94).

A short interhyal-metapterygoid ligament is present in all three groups.

No interhyal-preopercular ligament is present in any examined species of the three groups (*cf.* the other cirrhitoids described below).

A stout mandibulo-interopercular ligament (Fig. 1C; lig. 3) is present in taxa of the three groups. It is confined to the lateral face of both elements in all species except *Cyprinocirrhites polyactis* and *Cirrhichthys oxycephalus* (both members of Group I). In these two species it divides anteriorly to insert on both the lateral and the medial aspects of the anguloarticular bone.

Also common to species of the three groups is a short and deep, ventrally located ligament connecting the anguloarticular and dentary.

## The family Latridae

There are clear-cut differences in certain aspects of the ligamentous and other connective systems in the two latrid species examined, namely the monotypic genus *Mendosoma lineatum* (Gay) and the species *Acantholatrtris monodactylus* (Carmichael) of that polytypic genus. Also, an upper division of the adductor mandibulae muscle  $A_1$  is absent in *A. monodactylus* whereas in *Mendosoma* it is an elongate, rather thin element which lies lateral to the major part of the muscle and extends over the greater part of its length. The minor division, unlike the major one, has no direct connection with the ligamentum primordium and inserts on the maxilla, together with the major division, *via* the maxillary tendon of the  $A_1$  muscle.

In *Mendosoma* the adductor mandibulae Aw division is a very thin muscle, largely tendinous and with a single posterior extension of its tendinous aponeurosis. This runs slightly below the upper point of the articulation of the lower jaw with the quadrate, to which bone it is attached a short distance from the anterior border (Fig. 2; tendon 3). In other words, it is of the basic percomorph type *sensu* Gosline (1986), except that in *Mendosoma* it has one prolongation extending along the symplectic, another running ventrally to attach to the medial aspect of the preoperculum, a third, directed dorsally to insert on the quadrate, and a fourth directed obliquely backwards to attach to the ventral aspect of the interoperculum medially and anteriorly.

In all essentials, the adductor mandibulae Aw tendon system's extension onto the interoperculum and preoperculum in *Mendosoma* is very similar to that in *Acantholatrtris*, with that in *Mendosoma*, as it were, foreshadowing the more clearly differentiated condition in *Acantholatrtris* (*cf.* Figs 2 & 3).

There is no ligament-like connection between the mandible and hyoid arch in *Mendosoma* (*cf.* *Acantholatrtris*; Fig. 3).

The epihyal-interopercular ligament is stout and short, connecting the lateral aspect of the epihyal with the dorsal margin of the interoperculum a short distance anterior to its slightly raised facet for articulation with the epihyal. Unlike the backward-facing facet in those cirrhitids in which it occurs, that in *M. lineatum* faces forward (Fig. 2), as it does in the other latrid examined (*Acantholatrtris monodactylus*; and in the cheilodactylids dissected).

A discrete interhyal-interopercular ligament (present in cirrhitids) is apparently lacking in *M. lineatum* (as it is also in *Acantholatrtris*, and *Cheilodactylus*).

Like the two latter genera, but not in the cirrhitids examined, *Mendosoma* has a well-developed interhyal-preopercular ligament and another, more dorsally placed ligament between the interhyal and the metapterygoid (Fig.

2; fig. 7). This latter ligament I consider to be the homologue of the interhyal-quadrate ligament in *Cheilodactylus*, and the ligament in *Acantholatrtris* which runs from the interhyal to both the quadrate and the entopterygoid (see p. 98 & p. 99 respectively).

*Mendosoma* has discrete lateral and medial divisions of the mandibulo-interopercular ligament, with the medial division terminating a short distance behind the anterior tip of the interoperculum (Fig. 2; fig. 6), and the lateral division extending much further posteriorly.

The anguloarticular-dentary ligament is short and stout, markedly stouter than in any cirrhitid species examined, and stouter than that in *Acantholatrtris*.

As compared with the ligamentous and other connective tissue systems in *Mendosoma lineatum*, those in *Acantholatrtris monodactylus* are considerably more complex, (as they are when compared with the cirrhitid species studied). As was noted earlier (p. 94), there is no obvious sub-division of the adductor mandibulae  $A_1$  muscle in *A. monodactylus*. However, anteriorly the upper third of the muscle, unlike the other two-thirds, is free from the ligamentum primordium and inserts on the maxilla only through the maxillary tendon, to which the major part of the muscle is also attached.

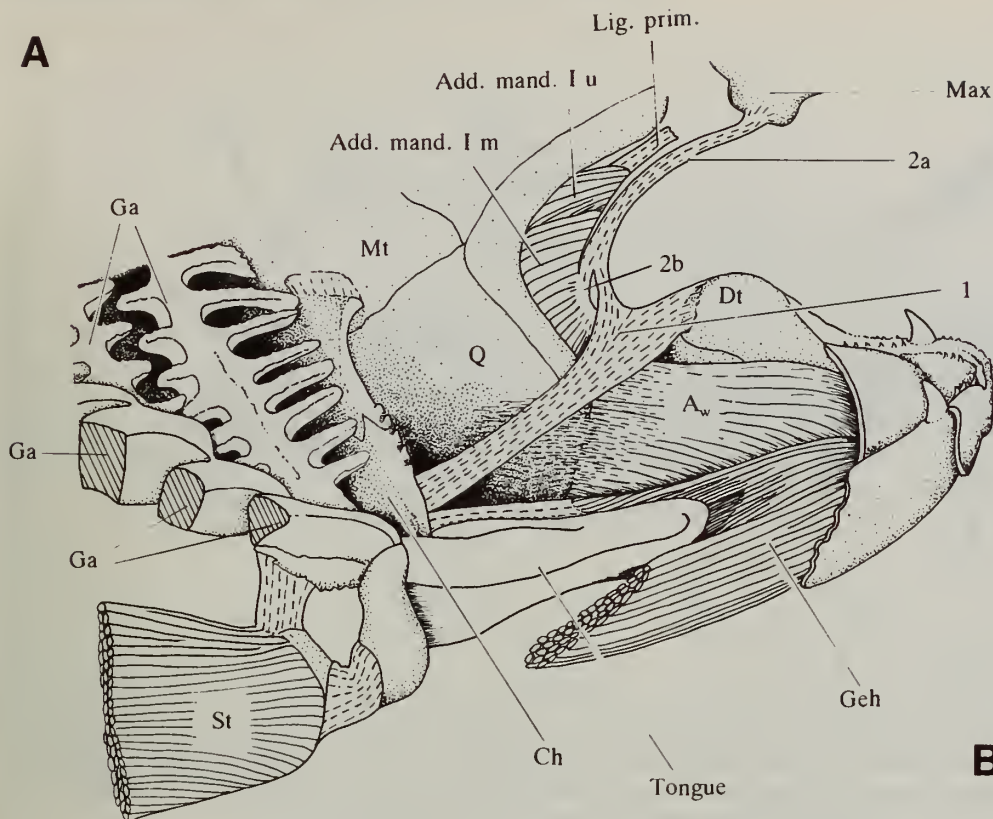
*Acantholatrtris monodactylus* has a substantial Aw portion of the adductor mandibulae muscle. From the muscle's mediolateral tendinous aponeurosis a stout and relatively short branch (tendon 3 in Fig. 3) runs posteriorly to insert on the anteromedial aspect of the preoperculum's horizontal limb.

A second stout and much longer tendon from the Aw muscle (tendon 5 in Fig. 3) extends from the ventral margin of the muscle above the anguloarticular bone, and runs obliquely backwards to attach to the medial aspect of the interoperculum a short distance from that bone's anterior tip. This tendon, unlike tendon 3, is not derived from the aponeurosis of the adductor mandibulae Aw muscle but originates directly from the muscle itself. Immediately after its origin, tendon 5 is attached to the anterodorsal aspect of the anguloarticular's medial face. It then passes over that face of the retroarticular, and attaches to the medial aspect of the interoperculum a short distance from the bone's anterior tip. Since this tendon links the mandible with the interoperculum it would appear to be the functional equivalent of the mandibulo-interopercular ligament in the other species described above. However, a true and very long mandibulo-interopercular ligament is also present in *A. monodactylus* (Fig. 3; fig. 6). Anteriorly it has an extensive attachment to the lateral face of the anguloarticular and retroarticular bones, as well as another on the posterior face of the retroarticular. From here the ligament extends across to, and

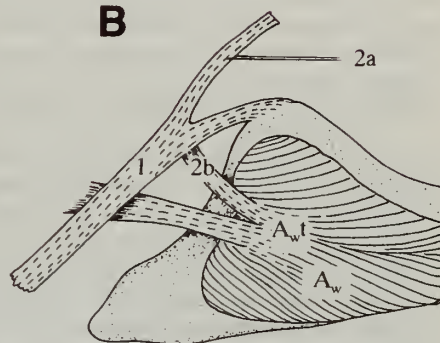
- Fig. 1** A: *Cyprinocirrhites polyactic* (Group I species) Medial aspect of the left lower jaw, cheek region and hyoid arch, viewed obliquely from above, to show the mandibulohyoid connection (semi-schematic). The branchial skeleton is displaced to the right. About times natural size. 1: Mandibulohyoid connection; 2a: tendon from lower part of adductor mandibulae  $A_1$  muscle to maxilla; 2b: continuation of tendon 2a, joining tendinous aponeurosis of adductor mandibulae muscle Aw. Lig. prim: Ligamentum primordium.
- B:** *Cirrhitops fasciatus* (Group I species) Diagrammatic representation of mandibulohyoid connection and related tendons; medial aspect of left side to demonstrate the second form of tendinous relationships within species of Group I. Abbreviations as in Fig. 1A.
- C:** *Paracirrhites forsteri* (Group II species). Medial aspect of the right lower jaw, cheek region and hyoid arch, viewed somewhat dorsally; the branchial skeleton and hyoid arch considerably displaced to the left and posteriorly in order to reveal the mandibulohyoid connection. (Semi-schematic). About times natural size. 1: Posterior portion of mandibulohyoid connection, inserting partly on the quadrate, and partly continuous with tendinous aponeurosis of the adductor mandibulae muscle Aw (Awt); 2b: ventral continuation of maxillary tendon of adductor mandibulae  $A_1$ ; 3: interopercular-mandibular ligament; 4: tendon of adductor mandibulae  $A_2$  muscle; Lig. prim: ligamentum primordium.



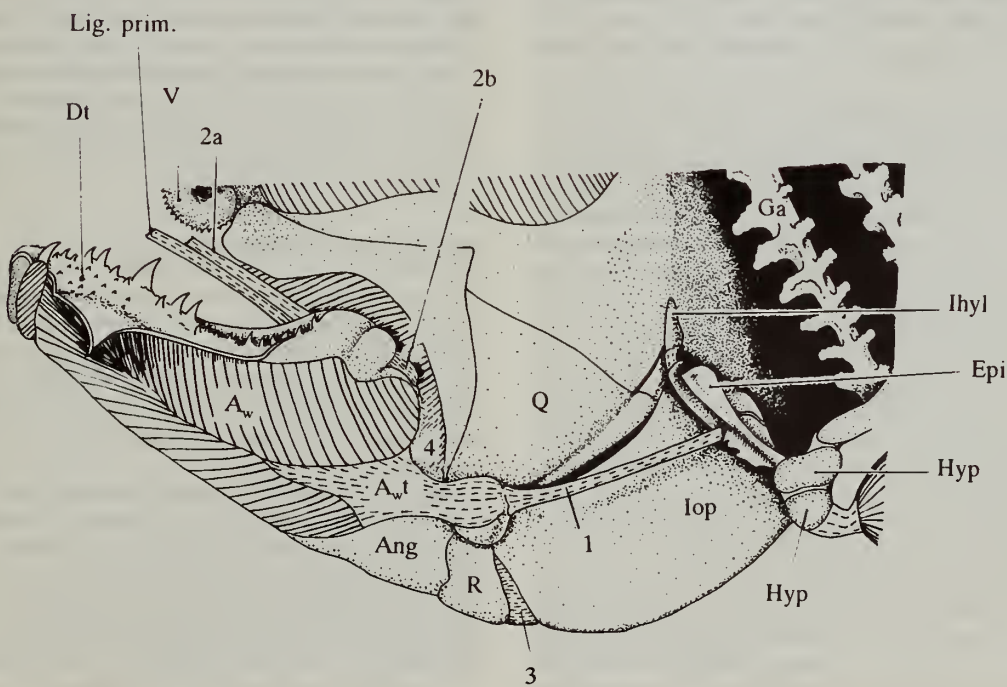
**A**

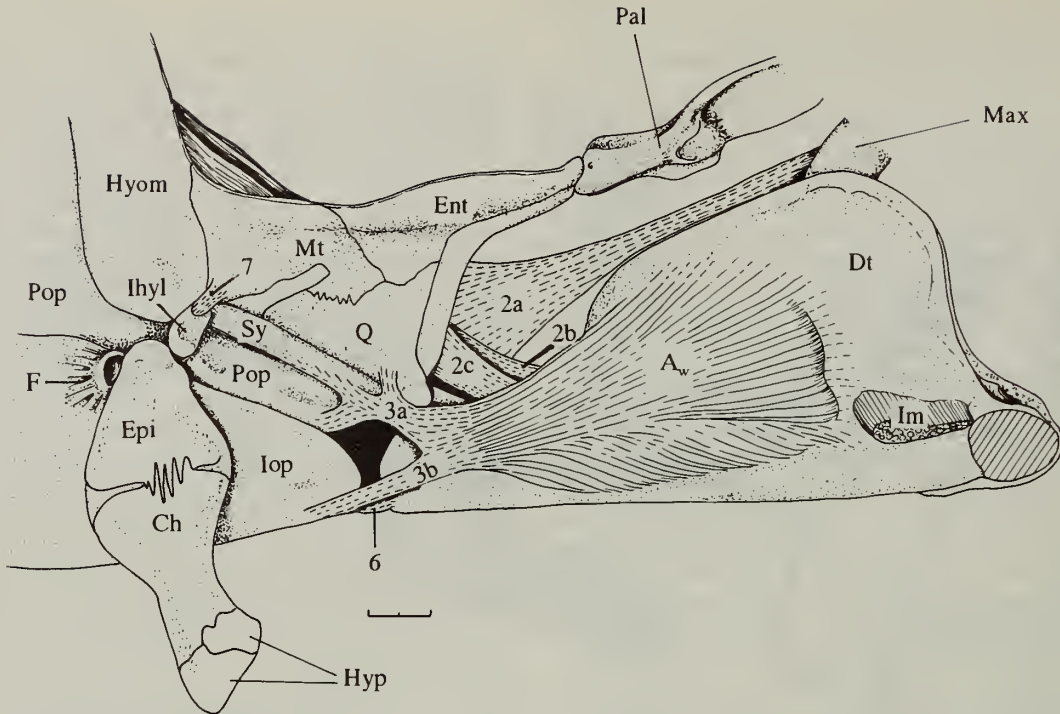


**B**



**C**





**Fig. 2** *Mendosoma lineatum* Medial aspect of left lower jaw, cheek region, and hyoid arch. Scale = 2mm. 2a: Maxillary tendon of adductor mandibulae muscle  $A_1$ ; 2b: extension of tendon 2a, joining tendinous aponeurosis of adductor mandibulae muscle  $A_w$ ; 2c: tendon of adductor mandibulae muscle  $A_2$ ; 3a & b: extensions of adductor mandibulae muscle  $A_w$ 's tendinous aponeurosis; 6: interopercular-mandibular ligament; 7: interhyal-metapterygoid ligament.

along, the dorsal and dorsolateral margins of the interoperculum, ending at a point about midway between the bone's anterior tip and the face of the prominent, forward-facing articular facet for the epihyal (cf pp. 94). Here it attaches to a slight eminence on the dorsal margin of the interoperculum. At first sight the ligament appears to be continuous with the epihyal-interopercular ligament (Fig. 3; fig. 4) which also inserts at that point. Careful dissection reveals, however, that the two are separate entities (see also p. 93 and p. 94 respectively for the situation in cirrhitids and the latrid *Mendosoma*).

Apart from the more complex condition in cheilodactylids, this double linkage of the mandible with the interoperculum, one involving both tendons and ligaments, seemingly has not been recorded in any other teleosts. However, it also occurs in *Mendosoma* (see p. 94 and Fig. 2) where the lowermost arm of the  $A_w$  aponeurosis is attached to the anteromedial aspect of the interoperculum, and in *Cheilodactylus* (see below, and tendon 5 in Fig. 4).

As in *Mendosoma*, the anguloarticular-dentary ligament in *A. monodactylus* is short and stout.

An elongate and broad ligament (fig. 7 in Fig. 3) connects the upper face of the interhyal with the quadrate and, mainly, with the entopterygoid. This connection is similar to that in *Cheilodactylus* (see Fig. 4, and p. 98), and, from its interconnections would appear to be homologous with the ligament joining the interhyal with the metapterygoid in *Mendosoma* (Fig. 2; fig. 7) and the cirrhitid species examined.

The interhyal-interopercular ligament, present in all members of the Cirrhitidae examined, is absent in the latrids and cheilodactylids dissected. An interhyal-preopercular ligament, present in the other cirrhitoids studied except the cirrhitids, is also developed in *Acantholatris*. Here, although

very short, it is stout and has an extensive attachment area on the interhyal and on the preoperculum, which it joins at the point where the upper, vertical arm of that bone begins to curve forward to form its horizontal arm.

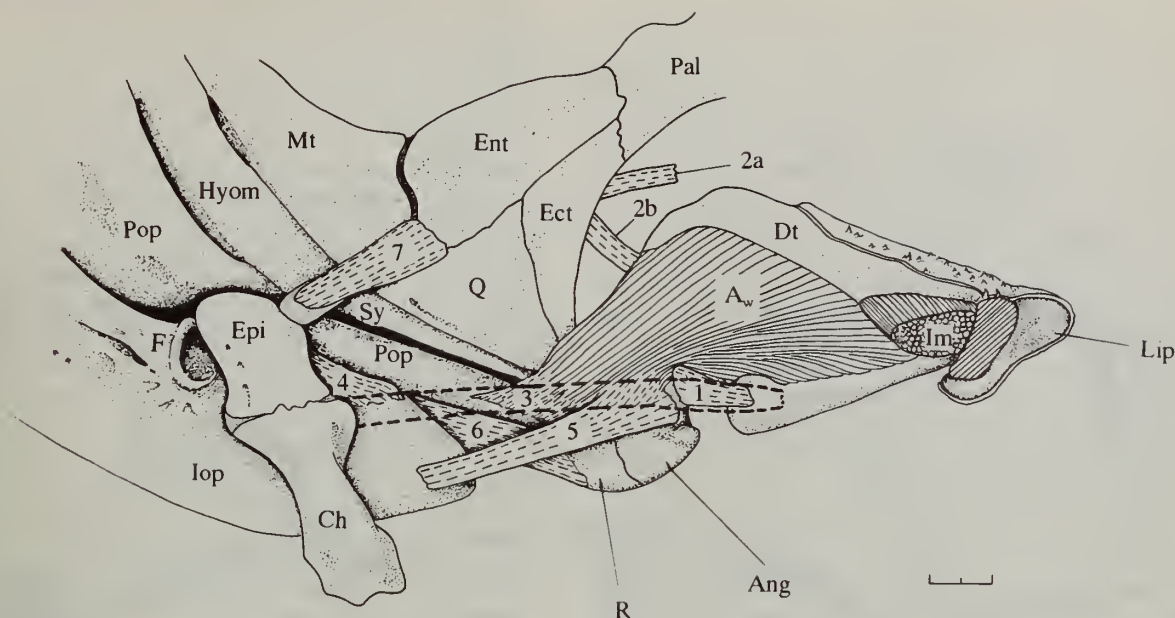
A feature unique to *Acantholatris monodactylus* amongst the cirrhitoid taxa examined is the presence of a well-defined ligament connecting the hyoid arch and the dentary, a linkage in no way associated with the adductor mandibulae  $A_w$  muscle or its aponeurotic system (see Fig. 3). Posteriorly, this ligament is attached to the summit of a distinct prominence on the anterior face of the ceratohyal and situated immediately below the ceratohyal-epihyal suture. Anteriorly, the ligament inserts on the dentary conjointly with the anterior end of the anguloarticular-dentary ligament (see above and Fig. 3; fig. 1).

### The family Cheilodactylidae

The account which follows is based on dissections of *Cheilodactylus fasciatus* Lacepède. Since the situation is virtually identical in two other cheilodactylid species studied, *Cheilodactylus pixi* (Smith) and *Chirodactylus brachydactylus* (Cuvier), the term *Cheilodactylus* is used to cover all three taxa. What interspecific differences do exist are noted on page 98.

Of all the cirrhitoid species examined, the ligament and tendon systems separately or conjointly linking the mandible, the hyoid arch, the opercular series, and the palatoquadrate arch in *Cheilodactylus* are by far the most complex. The greatest similarities, however, are with those systems in the latrid *Acantholatris monodactylus* (cf. Figs 3 & 4). In the cheilodactylids examined, and like *A. monodactylus*, there is no obvious subdivision of the adductor mandibulae  $A_1$





**Fig. 3** *Acantholatris monodactylus* Medial aspect of left lower jaw, cheek region and hyoid arch. Scale = 2mm. 1: Anguloarticular-dentary ligament; 2a: maxillary tendon of adductor mandibulae muscle  $A_1$ ; 2b: extension of above tendon joining tendinous aponeurosis of adductor mandibulae muscle  $A_w$ ; 3: tendon of  $A_w$  muscle to preoperculum; 4: epihyal-interopercular ligament; 5: tendon from  $A_w$  muscle to interoperculum; 6: interopercular-mandibular ligament; 7: interhyal-quadrate-entopterygoid ligament. Dashed outline that of the mandibulohyoid connection.

muscle, whose insertion on the maxilla is identical with that in the latter taxon.

The  $A_w$  portion of the adductor mandibulae muscle in *Cheilodactylus* is noticeably less extensive than in *Acantholatris*, but its tendinous connections with the interoperculum and the palatoquadrate arch are more complicated than in that taxon. Also, in *Cheilodactylus* the ventral extension of the adductor mandibulae  $A_1$  maxillary tendon is noticeably stouter than in *Acantholatris* (cf. Figs 3 & 4) but, unlike *Acantholatris*, in *Cheilodactylus* it is derived from the medial and not the lateral tendinous aponeurosis of the muscle's  $A_w$  division. A most obvious difference between the two taxa is the absence of a ligament connecting the hyoid arch with the mandible in *Cheilodactylus* (cf. Figs 3 & 4).

A somewhat tendinous section of the adductor mandibulae  $A_w$  division (tendon 3 in Fig. 4) in *Cheilodactylus* runs posteriorly, becoming completely tendinous as it crosses the hind margin of the anguloarticular and its joint with the quadrate. It inserts on the anterior tip of the preoperculum just below that bone's dorsal margin. At a point near the centre of the anguloarticular this partly tendinous section of the  $A_w$  division of the adductor mandibulae muscle gives off a ventroposteriorly directed branch which soon becomes completely tendinous. The anterior part of this tendon (5a in Fig. 4), immediately below its point of departure from tendon 3, is attached to the anguloarticular near its anterior margin. It thus lies below the bone's articulation with the quadrate. The posterior extension of tendon 5a runs backwards and somewhat dorsally, seemingly joining the lateral face of a broad, stout, dense, and obliquely orientated ligament-like strap (5b in Fig. 4) extending from the midpoint of the quadrate to the anteroventral surface of the interoperculum. Together the two elements (ie 5a and 5b in Fig. 4) form a 'Y' shaped linkage between the anguloarticular, quadrate, and interoperculum. Also, because the anterior arm of the 'Y' (ie

5a) is associated with an extension of the  $A_w$  muscle onto the anguloarticular, the linkage involves that bone as well.

Without ontogenetic information it is difficult to decide whether the element 5b of the 'Y' is, at it appears to be, a branch of the tendon 5a (and thus is itself a tendon) or whether it is strictly a ligament with which tendon 5a has fused. That none of the other cirrhitoids examined has a quadrato-interopercular ligament would add credence to 5b being a true branch of 5a, and thus representing a considerable posterior extension of the  $A_w$  muscle's tendon system. Also, in the other cheilodactylids examined, the 'Y'-shaped connection gives no hint of it having originated from a tendon and a ligament (see below). The potential complexity and posterior extension of that system is clearly demonstrated in another percomorph, the percid *Gymnocephalus cernua* (L.); see Elshoud-Oldenhave & Osse (1976; fig. 4.1).

When comparisons are made with the latrid *Acantholatris*, (see p. 94 and Fig. 3) it appears that the 'Y'-shaped complex in *Cheilodactylus* is, from its disposition and attachment points, homologous with the simple tendon (5 in Fig. 3) associated with the  $A_w$  portion of the adductor mandibulae muscle in *Acantholatris*. Tendon 5 in that taxon is attached to both the anguloarticular and the medial face of the interoperculum, and is separated by a short section of  $A_w$  from tendon 3 which inserts on the preoperculum (Fig. 3). In turn, and also from its disposition and points of attachment, the latter tendon would seem to be homologous with the longer tendon 3 in *Cheilodactylus* which also inserts on the preoperculum. An early evolutionary stage in the development of this complex in both *Cheilodactylus* and *Acantholatris* may be represented by the tripartite posterior extension of the  $A_w$  aponeurosis in *Mendosoma*, which also serves to link the  $A_w$  muscle with the quadrate, preoperculum and interoperculum (see p. 94 and Fig. 2).

The two other cheilodactylid species dissected, *Chirodacty-*

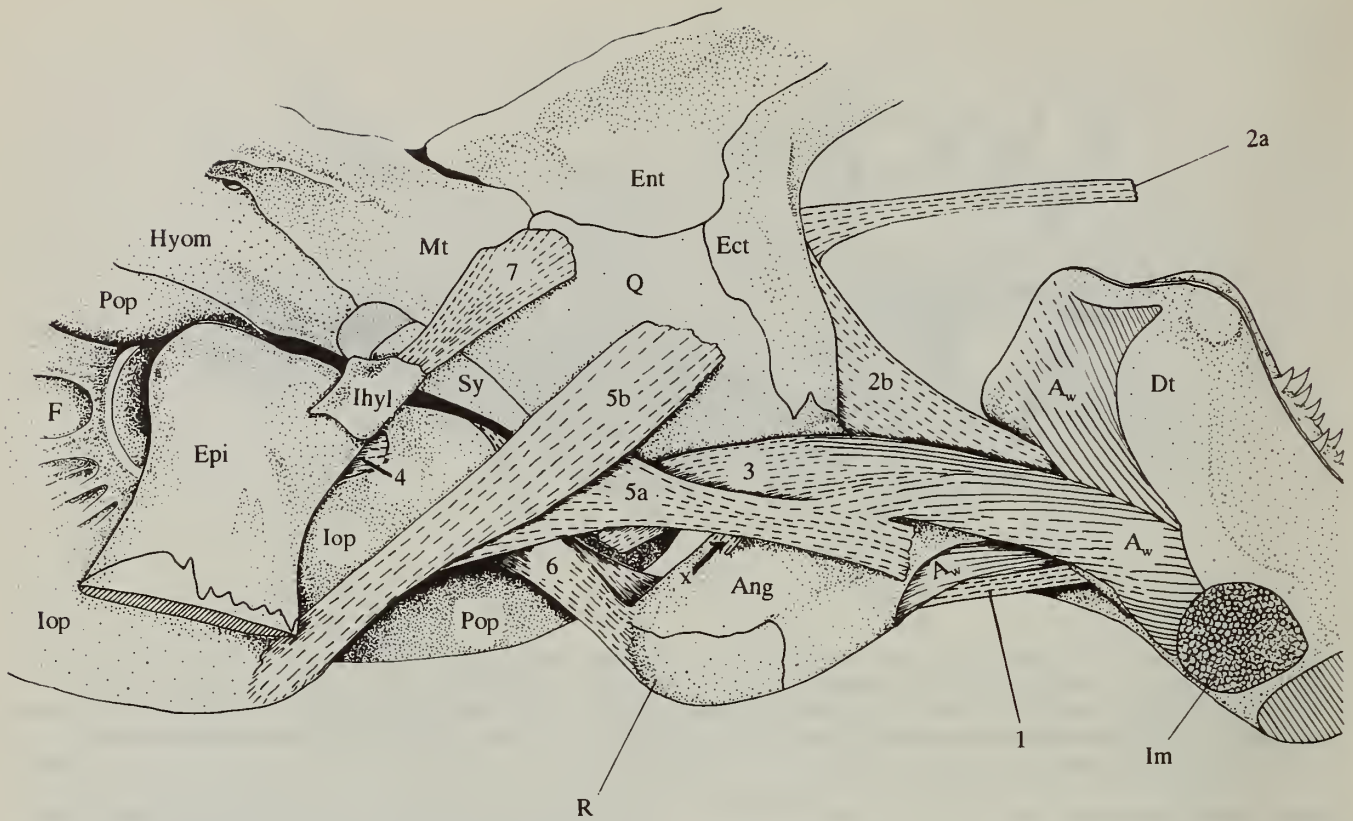


Fig. 4 *Cheilodactylus fasciatus* Medial aspect of left lower jaw, cheek region and hyoid arch. Scale = 2mm. 1: Anguloarticular-dentary ligament; 2a: maxillary tendon of adductor mandibulae muscle  $A_1$ ; 2b: extension of above tendon joining tendinous aponeurosis of adductor mandibulae muscle  $A_w$ ; 3: tendon of adductor mandibulae muscle  $A_w$  to preoperculum; 4: epihyal-interopercular ligament; 5a: extension of tendon 3; 5b: branch of tendon 5a, attaching to quadrate above and interoperculum below; 6: interopercular-mandibular ligament; 7: interhyal-quadrate ligament; x: anguloarticular-quadrate ligament.

*lus brachydactylus* and *Cheilodactylus pixi*, have a mandibular-preopercular-quadrate tendon system essentially like that described above in *Cheilodactylus fasciatus*. In these species the interopercular-quadrate branch (Fig. 4; 5b) does not partly overlap that section of the complex (Fig. 4; 5a) going to the anguloarticular. Instead, the two branches meet in the same plane, with the result that the complex is clearly single and 'Y'-shaped. Since the specimens of *Chirodactylus brachydactylus* (standard length 106 mm) and *Cheilodactylus pixi* (S.L. 70–81 mm) are much smaller than the specimen of *Cheilodactylus fasciatus* (S.L. 243 mm), the difference could be related either to the larger size of the *C. fasciatus* specimen or to individual variation.

The epihyal-interopercular ligament in *Cheilodactylus* is short and broad (shorter even than that in the latrid *Mendosoma*; and unlike the long and anteriorly directed ligament in the other latrid examined, *Acantholatris*, Fig. 4; lig. 4). As in *Acantholatris*, but unlike *Mendosoma*, the interopercular facet for the epihyal in *Cheilodactylus* is prominent and well-developed (see Fig. 4). The interhyal-quadrate ligament is long and flat (Fig. 4; lig. 7), again like that in *Acantholatris*, but unlike its presumed homologue, the short and stout interhyal-metapterygoid ligament in *Mendosoma*.

The interhyal-preopercular ligament in *Cheilodactylus* is also short and stout. No discrete interhyal-interopercular

ligament is developed in the cheilodactylids, a characteristic shared with the two latrid genera examined, but not with the cirrhitid species studied.

A stout anguloarticular-dentary ligament is present, as it is in the other cirrhitoids, but unlike those taxa *Cheilodactylus* has a short and broad ligament (x in Fig. 4) connecting the uppermost part of the anguloarticular's posteromedial face to the quadrate, where it is attached to the ventral rim of that bone's facet for articulation with the anguloarticular. This small ligament, not found in any of the other cirrhitoids examined, is almost entirely hidden by tendon 5a of the 'Y' shaped complex described above.

A very stout interopercular-mandibular ligament originates laterally on the dorsal margin of the interoperculum near its anterior tip, and inserts mostly on the lateral aspect of the anguloarticular and retroarticular bones, but with a short medial branch going to the posteromedial face of the retroarticular (6 in Fig. 4).

## DISCUSSION AND CONCLUSIONS

The taxonomically and phylogenetically widespread occur-



rence of a mandibulohyoid linkage in bony fishes (see Tchernavin, 1953, and references cited by Verraes, 1977, Springer *et al.*, 1877, Lauder & Liem, 1980, and above) certainly seems to support the views of functional anatomists with regard to its involvement in the mechanics of jaw opening. It also refutes the apparently widespread view (see reviews in Lauder & Liem, 1980; Lauder, 1982) that the linkage may be a primitive character of neopterygian fishes, one lost in higher teleosts (but see also Lauder & Liem, 1989, for later views). However, although the mandibulohyoid connection may be functionally homologous in both 'higher' and 'lower' bony fishes, there are indications that it may not be homologous in an ontogenetical and hence phylogenetic context (see below). Nevertheless, the diversity of mandibulohyoid connections already known in but a few teleost fishes strongly suggests that the structural, functional and ontogenetic aspects of this system need to be reevaluated.

Any attempt to establish or refute the homology of mandibulohyoid connections in cirrhitoid fishes with those in other bony fish groups (see below) is hampered by a lack of information on the ontogeny of the linkage in the various taxa involved. Indeed, this problem also arises with the different mandibulohyoid linkages found within the cirrhitoids themselves, namely those in the Cirrhitidae (p. 93) and that in the latrid *Acantholatris monodactylus* (p. 97).

The cirrhitid linkage type in the *Paracirrhites* species examined (p. 93) strongly suggests that the connection between the mandible and the ceratohyal in these fishes is derived from an extension of the central aponeurosis of the adductor mandibulae muscle's Aw portion onto the hyoid arch (with, in addition, a partial insertion on the quadrate; Fig. 1C and p. 93). In another cirrhitid group (*viz.* *Cypriocirrhites polyactis*, *Cirrhitichthys oxycephalus* and *Cirrhitops fasciatus*) the connection also has a linkage with the aponeurosis of adductor mandibulae Aw. Here it is effected, somewhat indirectly, by a branch from the major mandibulohyoid connection joining the maxillary tendon of adductor mandibulae A<sub>1</sub> muscle, which tendon itself is derived from the aponeurosis of the Aw portion of that muscle. This association with the Aw aponeurosis in both cirrhitid groups raises the possibility that ontogenetically, the mandibulohyoid linkage is through a tendon and not a ligament as it appears to be in the salmonid *Oncorhynchus mykiss* (see Verraes, 1977). It also raises the question whether or not the so-called mandibulohyoid ligament (see below) in other teleosts (and in the semionotiform Lepisosteidae; see below) is truly a ligament. A similar problem arises with the third type of mandibulohyoid connection found in cirrhitoids, namely that in the latrid *Acantholatris monodactylus*. Here the linkage is not associated with the Aw muscle, and has both its origin and its insertion entirely on bone, thus appearing to be a true ligament.

There is some indirect support for the idea that in members of the Cirrhitidae the mandibulohyoid connection could be derived ontogenetically from the adductor mandibulae muscle bloc (*sensu* Edgeworth, 1935) of the early embryo. This stems from the considerable posterior extension of the adductor mandibulae Aw aponeurosis onto the bones of both the palatoquadrate arch and the interoperculum in certain other perciform fishes (see also discussions in Winterbottom, 1974; Elshoud-Oldenhove & Osse, 1976; Anker, 1978; Greenwood, 1985) and, indeed in other cirrhitoids such as the cheilodactylids.

An origin of the mandibulohyoid connection from the

adductor mandibulae Aw tendon system seems less likely in the latrid *Acantholatris monodactylus*. Here the linkage extends from the posterior tip of the dentary's lower arm (not, as in the cirrhitids, from its coronoid process or the anguloarticular) to the upper part of the ceratohyal's lateral face (Fig. 3). At no point has this apparent ligament in *Acantholatris* any association with the adductor Aw muscle or any part of its tendon system. With regard to its attachment to the lower aspect of the dentary, the connection is comparable both with the loosely compacted and fibrous linkage between the dentary and ceratohyal identified by Aerts *et al.* (1987) in the cichlid *Astatotilapia elegans*, and with Osse's (1969) ligament XXIV in the percid *Perca fluviatilis*. In both these species, however, the tissue has insertions on certain branchiostegal rays as well as on the ceratohyal, and in neither species does it have the ligament-like appearance of the connection in *Acantholatris monodactylus*.

Aerts *et al.* (1987:97) describe in some detail the histology of the hyoid-dentary connection in *Astatotilapia elegans*, which seemingly is derived from the anterior, tendinous part of the geniohyoideus muscle, with whose dorsolateral aspect it is closely associated over much of its length. These authors conclude (*op. cit.*: 99) that 'In fact, the rostral part of the interconnection can be interpreted as a parallel elastic component of the protractor hyoidei' (=geniohyoideus). The posterior attachment of the connection is on the epi- and ceratohyals dorsally, with, as noted above, a number of small strands merging into the dermal layers of the skin-fold between the hyoid and interoperculum. A mandibulohyoid connection, superficially like that in *A. elegans* also occurs (*pers. obs.*) in another haplochromine cichlid, *Thoracochromis buysi* (Penrith); although its histology was not studied, the linkage appears to originate from within the geniohyoid muscle, and to attach to the hyoid arch at the epi-ceratohyal suture.

At least with regard to its superficial features, Aerts *et al.*'s description of the dentary-hyoid connection in *Astatotilapia elegans* does not resemble the condition seen in *Acantholatris monodactylus*. Here, the interconnecting tissue is clearly separated from the geniohyoideus muscle over virtually its entire length, and is much more compact and ligament-like. However, posteriorly it does appear to fuse with the tendinous insertion of the geniohyoideus at the point where both elements attach to an elevation on the anterior margin of the ceratohyal. The insertion of the geniohyoideus muscle then extends down along the lateral face of the ceratohyal, but that of the mandibulohyoid connection does not. Thus in adult *Acantholatris monodactylus* the only suggestion of the connection being derived from the geniohyoideus muscle is a partially shared insertion with that muscle on the ceratohyal. That suggestion is, unquestionably, far less convincing than the evidence provided by the situation in *Astatotilapia elegans*, but is one that could be clarified if studied ontogenetically in *Acantholatris monodactylus*.

A distinct mandibulohyoid ligament, superficially like that in *Acantholatris monodactylus*, has been described by Wiley (1976) in the semionotiform gars *Lepisosteus* and *Atractosteus*. The connection is labeled as a tendon in figure 9 of Wiley's paper, but is referred to, I believe correctly, as a ligament in the accompanying text. The ligament in gars differs from the ligament-like mandibulohyoid connection in *Acantholatris monodactylus* in its points of attachment (epihyal and retroarticular in the gars, ceratohyal and dentary in *A. monodactylus*). Again, without ontogenetic information



from both taxa, nothing can be said about its possible homology in the two species.

The concept that a mandibulohyoid connection (usually referred to as a ligament) is essentially a feature of pre- and lower teleost actinopterygians, has influenced theories relating to the evolution of feeding mechanisms in teleosts. For example, Lauder (1982: 279, also fig. 1) postulated that 'The first specialization involves a shift of insertion of the mandibulohyoid ligament to the interoperculum. The interoperculo-hyoid ligament characterizes the feeding mechanism of eurypterygian fishes (=Aulopiformes + Myctophiformes + Paracanthopterygii + Acanthopterygii; Rosen, 1973) and effectively shifts the action of the hyoid and opercular coupling onto the interoperculum. Only the interoperculo-mandibular ligament transmits posterodorsal hyoid and opercular movements to the mandible in the Eurypterygii, while other teleosts retain the primitive two-coupling system of the halecostomes' (*ie* both a mandibulohyoid and an interopercular-mandibular linkage). Verraes' (1977) studies on the development of *Oncorhynchus mykiss* show unequivocally that in this teleost there is no ontogenetic shift of the mandibulohyoid ligament's mandibular insertion onto the interoperculum. Indeed, the interopercular-mandibular ligament develops independently (and later than the mandibulohyoid ligament) with both connections persisting in adults (Verraes, 1977; pers. obs.); neither is there any ontogenetic evidence to show that the epi- (or inter-) hyal to interoperculum ligament is the result of a preexisting mandibulohyoid ligament shifting its mandibular insertion onto the interoperculum. Interestingly in that context, the latrid *Acantholatris*, which has what appears to be a genuine mandibulohyoid ligament (see p. 97) also has an epihyal-interopercular ligament.

Thus, *pace* Lauder (1982), it would seem that cirrhitoids (and other teleosts) with both a mandibulohyoid connection and an interopercular-mandibular ligament have either retained the primitive halecostome condition or, as seems more likely, re-evolved it through some other form of connective tissue linkage between the hyoid arch and the mandible.

Parenthetically, it may be noted that the importance of an interopercular-mandibular linkage in the jaw-opening mechanism of teleosts, stressed by Lauder *op.cit.* and other authors (see for example Liem, 1978 & 1991; Aerts *et al.*, 1987, and references therein) is underlined, albeit indirectly, by the condition in three of the cirrhitoid taxa examined. In *Cheilodactylus* (Cheilodactylidae) and in *Mendosoma* and *Acantholatris* (Latridae) there is, in addition to the interopercular-mandibular ligament a second such linkage effected through an extension of the Aw muscle's aponeurotic system onto the interoperculum (see pp. 94 & 97 and Figs 2-4).

If, as suggested above, certain teleosts have re-evolved a mandibulohyoid connection, it may have arisen in different ways. This seems probable even within the cirrhitoids (*viz.* cirrhitid and latrid types; see pp. 93 & 94), and in other groups as well. In the ostariophysan *Hydrocynus vittatus* (Characidae) for example, the mandibulohyoid connection appears to be an extension of the epihyal-interopercular ligament which, after its insertion on the dorsal margin of the interoperculum, continues forward to bridge the small gap between that bone and the retroarticular (pers. obs.). The salmonid *Oncorhynchus mykiss*, by contrast, has no obvious association of the mandibulohyoid connection with the epihyal-interopercular ligament. Both are discrete entities

throughout their lengths despite having insertion points close together on the epihyal (pers. obs.). The clupeid *Etrumeus*, unlike the preceding examples, has no readily discernible mandibulohyoid connection. However, the geniohyoideus muscle has a thickened and tendinous dorsal margin which is macroscopically continuous with the muscle from the latter's origin near the dentary symphysis to its insertion immediately over the epi-cerato-hyal suture (pers. obs.). Superficially at least, the situation in this clupeid shares certain similarities with the mandibulohyoid link in the perciform cichlid *Astatotilapia elegans* (see Aerts *et al.*, 1987, and p. 99 above). In the clupeid, however, the differentiation of the linkage from the associated muscle is at a somewhat lower level of development than that in the cichlid.

Verraes (1977) highlighted the functional importance of the mandibulohyoid connection in immediately post-hatching stages of the salmonid *Oncorhynchus mykiss*. This apparently ligamentous connection develops earlier than the interopercular-mandibular ligament. Thus at this point in the fish's life-history it is an essential element in bringing about jaw depression, and consequently it plays a major role in the creation of the trans-buccal water current involved in respiration and feeding (see also Lauder & Liem [1989] for a discussion of this ligament in the feeding mechanism of another salmonid, *Salvelinus fontinalis*). Recently, Aerts *et al.*, (1987), working with the cichlid *Astatotilapia elegans*, postulated that a mandibulohyoid connection is also of crucial importance in the feeding mechanism in adults of that species.

Regretably, no experiential work has been carried out on the feeding mechanisms of cirrhitoid fishes, nor is there enough critical information on their feeding habits to determine what correlations may or may not exist between species with or without a mandibulohyoid connection. It would be interesting to know in what way the mandibulohyoid connection functions in cirrhitids such as *Cyprinocirrhites polyactis*. Judging from preserved specimens it would seem to block the sinking of the lower jaw when the hyoid is pulled posteriorly by the contracting sternohyoideus muscle – a somewhat anomalous situation, but possibly one that may be associated with a specialized suction mode of feeding on small crustacean zooplankters, apparently the principal food of this species in South African waters.

As yet, the intrabuccal tendon and ligament systems are known from too few cirrhitoid taxa to test its usefulness in the intragroup taxonomy and phyletic relationships of those fishes. However, the tendon system in the Cheilodactylidae examined, when compared with that in the latrid *Acantholatris monodactylus* (cf. Figs 4 & 3) supports the latter taxon's removal (see Greenwood, 1995) from the genus *Cheilodactylus* and the family Cheilodactylidae in which it had been placed previously. Those differences also provide an additional character complex for distinguishing the Latridae from the Cheilodactylidae.

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